NOTES ON THE ANATOMY OF *HANLEYA ABYSSORUM*, M. Sars.

By R. H. Burne, B.A.,
Assistant in the Museum of the Royal College of Surgeons of England.

Read 8th November, 1895.

PLATE II.

1. On the probable Presence and Position of an Osphradium.

An osphradium, it need scarcely be said, is the name given by Professor Ray Lankester[1] to a sense organ, presumably olfactory, situated at the base of the gills in molluscs; it reaches its greatest development among the Prosobranchs, where it assumes a bipectinate gill-like form constituting the well-known "false branchia." The original discovery of this organ in isolated instances, although interesting, is practically of small moment, for it was not till 1881 that it emerged from the obscurity of isolation, to rank as one of the most important of molluscan organs. In that year Spengel[2] issued an important paper on the relationships existing between the various orders of the Mollusca, in which he pointed out the constancy of the occurrence and position of this olfactory organ in a great number of instances, and from this constancy was led to infer the unity of origin of the entire phylum. His wisdom in basing so great a generalization upon such a foundation has been called in question, as was almost inevitable; but from the favour with which his views are received in many quarters, especially, I believe, in England, we are amply justified in regarding this sense organ as one possessing somewhat exceptional interest, not only for students of the Mollusca, but for zoologists generally.

Such being the case, one cannot but regret to find that among the Chitons—molluscs that, on account of their many archaic characteristics, are justly considered to possess a fundamental importance—the exact position, and even the presence, of this organ are subjects still enveloped in doubt.

The following brief historical survey will display the present state of our knowledge, or rather ignorance, upon this point.

As far as I am aware, Spengel in 1881[3] was the first to suggest the presence of an osphradium in Chiton, but unfortunately it was only a suggestion based upon superficial observation. As sundry Chitons crawled up the sides of an aquarium, he noticed upon the outer side of each gill a brownish patch, the position and general appearance of which were strongly suggestive of an osphradium; and as such, Spengel was inclined to regard it; but although he emphasizes

[1] Encycl. Brit., article "Mollusca."

[2] J. W. Spengel, "Die Geruchsorgane und das Nervensystem der Mollusken": Zeitschr. Wiss. Zool., xxxv, 1881, p. 338.

[3] *Loc. cit.* p. 356.

the importance of this organ, especially for the determination of the true nature of the gills, he apparently did not at the time enter upon an examination of its detailed structure. Two years later the matter was investigated by Béla Haller[1] in the course of an exhaustive inquiry into the anatomy of two species of *Chiton* (*C. siculus*, Gray, and *C. fascicularis*, Poli). He was unable to confirm Spengel's suggestion. In transverse sections of the gills he observed that, although the epithelial cells covering the outer walls of both branchial vessels were slightly larger than those upon other portions of the gill, and were provided with enormous cilia, yet there was no marked local epithelial thickening characteristic of an osphradium, and no pigment cells. The absence of the latter, and the strongly pigmented nature of the blood, led him to suppose that probably Spengel had been deceived by the pigmented appearance given to the living tissues by the blood. This is practically the last we hear of Spengel's osphradium on the outer surface of the gill. The subject was revived again in 1891 by Blumrich,[2] who devotes some pages to the description of an organ, which he regards as the osphradium, situated this time not on the outer but on the inner side of the gill. The organ consists essentially of two ridges of lofty epithelium extending from the first to behind the last gill: one ridge (parietal) is situated on the body-wall; the other (paraneural) beneath the lateral nerve-cord, extending somewhat on to the surface of each gill. The epithelium consists of large glandular cells and hair cells; the latter are specially concentrated in certain positions, forming sensory knobs; in some species the ridges may vanish, leaving only the knobs; the hair cells are in communication with the lateral nerve-cords. The lining of the genital duct is continuous with the paraneural ridge. These tracts of modified epithelium were originally described by Haller,[3] but were considered by him to be glandular in function and not sensory. The true meaning of this epithelium is doubtful, for Haller[4] still persists in his original view, laying stress on the close relationship between the ridges and the genital ducts, and pointing out that most probably it is homologous to the hypobranchial gland of Prosobranchs. Thiele[5] also is unconvinced by Blumrich's observations. On the other hand Simroth,[6] taking an impartial survey of the question, considers that Blumrich's interpretation is probably correct; and this view has also been adopted by Lang,[7] although he does not discuss the matter.

During the spring of the present year, three specimens of *Hanleya*

---

[1] B. Haller, "Die Organisation der Chitonen der Adria." Pt. 2: Arb. Inst. Wien, v, 1883, p. 26.

[2] J. Blumrich, "Das Integument der Chitonen": Zeitschr. Wiss. Zool., lii, 1891, p. 460.

[3] *Loc. cit.* p. 21.

[4] Haller, "Beiträge zur Kenntnis der Placophoren": Morph. Jahrb., xxi, 1894, p. 34.

[5] Thiele, "Beiträge zur Kenntnis der Mollusken": Zeitschr. Wiss. Zool., liii, 1892, p. 586.

[6] Bronn's Klassen und Ordnungen des Thier-reichs, Bd. iii, Mollusca, 1894, p. 262.

[7] A. Lang, Lehrbuch der vergleichenden Anatomie, 1888–94, p. 744.

abyssorum, a Chiton found at a depth of from 150 to 200 fathoms off the coast of Norway, were bought for the Royal College of Surgeons. After dissecting these specimens for the purposes of the Museum, it seemed desirable to confirm certain details by the examination of microscopic sections made from the remaining fragments. These sections, cut with the object of verifying certain points in the respective shape and size of different regions of the lateral nerve-cords, revealed upon investigation, as so often happens, other points of interest besides those actually expected, throwing in this instance considerable light upon the vexed osphradial question.

The individual gills of a Chiton are innervated from the lateral nerve-cord by means of a pair of fine nerves, one of which runs down the outer wall of each blood-vessel.[1] Both nerves, in contradistinction to the lateral cords from which they spring, are entirely devoid of ganglion cells. Although such an arrangement is the general rule, it does not hold in the case of *Hanleya abyssorum*, except for the three anterior gills; for in that Chiton, from the fourth gill to the sixteenth and last, the outer branchial nerve, that is the nerve situated in the wall of the efferent branchial vessel, is ganglionated in varying degrees (Fig. I, iv–xvi). In the fourth and fifth gills the ganglion cells are confined to the proximal portion of the nerve, forming a small oval ganglion, lying without the gill on the floor of the main efferent branchial vessel. From the sixth gill onwards ganglion cells are present upon the nerve, both before and after its passage from the main efferent branchial vessel into the individual vessel of the gill. The maximum number of ganglion cells is reached about the tenth gill, and from that point to the sixteenth gill the size and extent of the ganglionic masses have a slight tendency to diminish. Looking closer at a well-marked example, say the tenth gill, it will be noticed (Pl. II, Fig. 1, *e.n.*) that the ganglion cells are not evenly distributed over the entire surface of the nerve, as in the cords of the central nervous system, but are aggregated into patches, thus forming a string of ganglionic enlargements, giving the nerve a beaded appearance. In the first ganglion, the one, that is, lying without the gill in the main efferent branchial vessel (Pl. II, Fig. 1, *gg.*), the ganglion cells form a cortex surrounding a central bundle of fibres, but in the portion of the nerve situated within the gill they are chiefly confined to the surface directed towards the cavity of the blood-vessel (Pl. II, Fig. 2, *e.n.*). The ganglion cells in question are small, closely congregated together, and provided with a round nucleus, thus agreeing with the cells that are considered to be characteristic of a *sensory* ganglion.[2] The side of the nerve directed towards the exterior is fibrous in structure, and is closely applied to the epithelial covering of the blood-vessel. Before leaving the nerves and turning to the epithelium, I wish to draw attention to a slight peculiarity of the lateral nerve-cord itself: it will

[1] An idea of the general anatomy can be obtained from Pl. II, Fig. 1.

[2] J. Thiele, "Ueber Sinnesorgane der Seitenlinie und das Nervensystem von Mollusken": Zeitschr. Wiss. Zool., xlix, 1890, p. 425.

be seen on referring to Fig. I, that in its anterior part, in fact till it arrives at the region of the gills (confined in this species to the hinder part of the body), it is circular in cross-section; at that point it becomes distinctly larger, broader, and flatter, and though this enlargement is not very striking, yet it is sufficiently so to be suggestive of a tendency to concentration in this region, a tendency that may be due, no doubt, to the restricted area occupied by the gills.

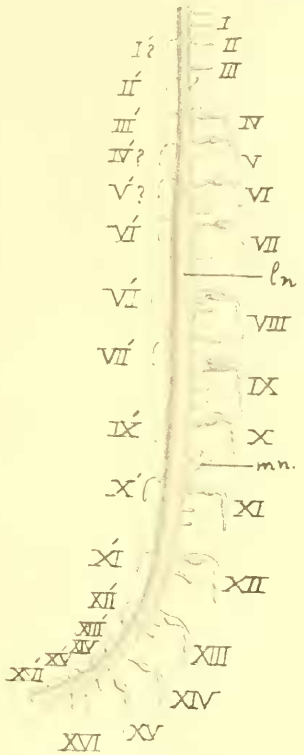

Fig. I.—Posterior portion of the right lateral nerve-cord of *Hanleya abyssorum*. × 8 (reconstructed from sections). *l.n.* lateral nerve-cord. *m.n* mantle nerves. i-xvi. external branchial nerves. i'-xvi'. internal branchial nerves.

We will now turn to the epithelial covering of the efferent branchial blood-vessel. In spite of the necessarily imperfect condition of such delicate tissues, in specimens preserved merely in spirit, a transverse section makes it sufficiently clear that its structure does not entirely tally with the description given by Haller.[1] Apart from the enormous

[1] *Loc. cit.* p. 26.

cilia, which one could hardly expect to see in material so preserved, the epithelium, instead of consisting of a single row of cells of a slightly larger size than those covering the surrounding parts, is considerably thickened at the anterior and posterior margins of the vessel, and in these localities is apparently composed of more than one row of cells, for the nuclei are arranged in two fairly distinct layers—a distal row of regularly disposed nuclei continuous with those of the low epithelium of the gill lamellæ, and an irregularly scattered proximal layer (Pl. II, Fig. 2, *ep.*). In the central portion of the blood-vessel the epithelium resumes its low, single-layered condition. The ganglionated nerve-cord lies beneath the anterior thickening.

It would be rash to give any definite opinion upon the nature of this epithelium, but this much one may say with safety—Its structure is not repugnant to the idea that it may possess a sensory function, for the distal row of nuclei may very possibly belong to indifferent supporting cells, and the proximal scattered layer is somewhat suggestive of hair cells packed between the supporting cells; then, again, the local thickening of the epithelium would be in perfect harmony with such a view. Of course the sensory nature of this epithelium is the vaguest of possibilities, if we consider the epithelium by itself alone; but when taken in conjunction with the presence of a nerve-cord close beneath it, richly endowed with sensory ganglion cells, the possibility becomes so strong a probability that I think we may with some confidence regard this complex of lofty epithelium and ganglion as a sensory organ, in all probability an osphradium.

With the hope of gaining further knowledge on this point, it seemed desirable to examine the gills of some other species of Chiton which could be obtained in a state more suitable for the microscope; I therefore procured some specimens of *Acanthochites discrepans* (Brown), a fair-sized Chiton occurring among the Channel Islands. In this mollusc the gills are not restricted so entirely to the hinder region as in *Hanleya abyssorum*, but extend backwards from about the middle of the body, gradually increasing in size from the anterior end. When examined with a pocket lens, there can be seen running down the efferent branchial vessel of each gill a narrow brown line, which recalls to the mind Spengel's brown patch, with this difference, however, that whereas his was a diffuse patch, this is a hard narrow line, which is fairly distinct at the base and gradually becomes fainter as it approaches the tip of the gill.

A transverse section of one of the gills shows that this brown line is due to a narrow ridge of elevated pigmented epithelium surmounting the nerve, and following its course for a considerable distance towards the point of the gill.

The detailed structure of this epithelium (Pl. II, Fig. 3, *p.ep.*), as far as I have been able to make it out, leaves little doubt as to its nature, for it appears to consist of narrow hair cells packed into the interspaces between large pigmented supporting cells, a condition highly characteristic of a sensory epithelium. The supporting cells are somewhat conical in shape; the base of the cone is directed towards the exterior, and is the portion of the cell richest in pigments. The hair

cells, for such, on comparison with Bernard's[1] figures, I take certain dark staining streaks lying between the supporting cells to be, occur chiefly in this strip of elevated epithelium, but are also scattered throughout the low epithelium covering the rest of the walls of the blood-vessels.

The locality, pigmentation, and minute structure of this strip of elevated epithelium, when added to the ganglionic character of the external branchial nerve of *Hanleya abyssorum*, appear to warrant us in regarding this region of the gill as the seat of a sense organ, in all probability the representative of the osphradium in more highly specialized molluscs. The fact that the hair cells are not strictly confined to this modified portion of the epithelium suggests a certain diffuse sensibility, a condition in accord with the well-known lack of centralization in archaic creatures.

Although the general structure of this sense organ corresponds to that of an osphradium, yet before we conclude that such is indeed its nature, there are two considerable objections that must be mentioned. In the first place it is related to the wrong branchial vessel; in all cases the osphradium is in connection with the afferent branchial vessel, whereas this organ is on the efferent. With reference to this difficulty, it may be worth noting that a sense organ for testing the purity of the water would probably be so situated as to be most easily and rapidly accessible to the stream of water coming to the gills, a condition realized more nearly on the outside than on the inside of the gill; but whether such a change of position in a very constant organ can depend on so slight a physiological advantage may very well be doubted. The second difficulty occurs in the relations borne by the lateral nerve-cord to the viscera. Among the higher molluscs an osphradium invariably receives its nerve supply from the visceral loop, a nervous loop passing from one pleural ganglion to the other, situated morphologically entirely beneath the intestine. The lateral nerve-cord of Chiton, however, which from its relations to this assumed osphradium would be homologous to the visceral loop, passes above, not beneath the viscera.

This latter difficulty can, of course, be met by a supposed migration of the anus during the course of evolution; but perhaps a less violent escape is afforded by Hubrecht's[2] ingenious suggestion that possibly the posterior pedal commissure lost its original connection with the pedal cords, but remained united to the lateral by a pair of stout latero-pedal connectives; at the same time the normal posterior union of the lateral cords degenerated and vanished, thus transforming a dorsal into a ventral loop. Either of these alternatives is possible, but the magnitude of the assumptions necessary would excuse a certain amount of scepticism with regard to their probability.

If, in spite of these two difficulties—difficulties, I may add, which

---

[1] F. Bernard, "Sur les Organes Palléaux des Prosobranches": Ann. Sci. nat. 1890.

[2] A. A. W. Hubrecht, "*Proneomenia Sluiteri*": Niederl. Arch. Zool. 1881, p. 25.

neither prevented Spengel[1] from suggesting, nor Lankester[2] from accepting, the possible presence of an osphradium upon this identical spot—we decide to regard the sense organ in question as the representative of an osphradium, this will be a suitable place to very briefly indicate the influence that an osphradium would possess in regard to one or two questions of Chiton morphology.

Passing over the interest attached to the mere occurrence of the organ among the Amphineura, the first question with which an osphradium is concerned is the nature of the gills. Now, although it is usually held that in a Chiton each separate gill is a ctenidium complete in itself, it has been lately maintained that this is not the case,[3] but that the gills of a Chiton are processes of the mantle, organs of the lateral line homologous to the sense organs on the epipodium of the Rhipidoglossa and on the mantle of the Lamellibranchs. The presence of an osphradium (if we accept Spengel's view) would at once set this question at rest, for an osphradium is a constant adjunct of a ctenidium. In speaking of this point we have entered an outlying region of the epipodial controversy, a dispute that naturally suggests another important matter in connection with the osphradium, namely, the nature of the loop formed by the lateral nerve-cords. There are, I fancy, four alternative homologies: it may be considered as homologous to either—(1) the sensory ganglia in the epipodium of Rhipidoglossa, the pallial nerve of Lamellibranchs,[4] etc.; or (2) the outer division of the pedal nerve-cord of *Haliotis*,[5] if such a division exists; or (3) the pleural ganglia and anterior pallial nerves of Anisopleura and Lamellibranchs[6]; or, finally, the visceral loop of other molluscs.[7] The presence of an osphradium enforces our acceptance of the last alternative, on account of the constant innervation of the ctenidium and its associated osphradium from the visceral loop.

Such are the reasons, as far as I have been able to ascertain them, that tell both for and against the sensory and osphradial nature of this organ in the above two species of Chiton; and it must be left to others to judge whether the approximate situation and highly characteristic structure of an osphradium are to be outweighed by certain anomalous details of position[8] and innervation.

2. Further Notes on the Anatomy of *Hanleya abyssorum*.

(*a*) *The anterior buccal commissure.*—The condition of the buccal commissures in this species owes a great part of its interest to the conflicting statements that have been made with regard to this point

[1] *Loc. cit.* p. 356. [2] *Loc. cit.*

[3] Thiele, "Ueber Sinnesorgan . . . von Mollusken," etc.: Zeitschr. Wiss. Zool., xlix, 1890, p. 411.

[4] *Ibid.*

[5] H. v. Jhering, Morph. Jahrb., iii, 1877, p. 172.

[6] P. Pelseneer, "Sur l'epipodium des Mollusques": Bull. Sci. France et Belge, 1891.

[7] Spengel, *loc. cit.* p. 353.

[8] In this connection the wide separation of the osphradium from its associated gill in *Ampullaria* should be noted.

in different species of Chiton. Brandt,[1] in *Chiton fascicularis*, and later, Von Jhering,[2] in *Chiton squamosus*, described two commissures uniting the buccal ganglia to one another—a posterior passing, as usual, between the œsophagus and the radula sheath; and an anterior connecting the buccal ganglia across the anterior region of the roof of the buccal chamber. Béla Haller,[3] on the contrary, says that in *Chiton fascicularis* and *C. sieulus* there is no anterior commissure, and that it was probably an erroneous observation of the œsophageal nerves that led Brandt and Von Jhering to the description of a non-existent structure.

From my dissections of this region in *Hanleya abyssorum*, there seems to be no doubt that the latter observers were not mistaken; in this species the anterior commissure is not only easily traced from ganglion to ganglion, but the whole thing can, with a little care, be removed entire[4] (Fig. II, *a.b.c.*). I have also seen this

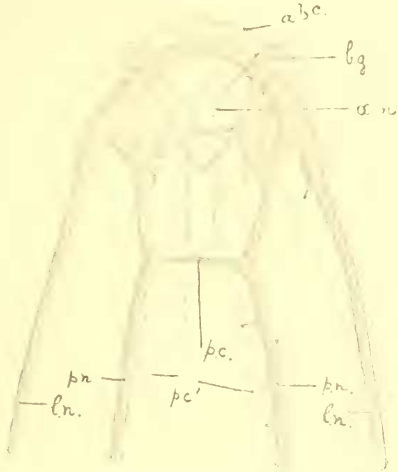

FIG. II.—Anterior portion of nervous system of *Hanleya abyssorum*. × 4. From Nos. 1305 C and D. R.C.S. *a.b.c.* anterior buccal commissure. *b.g.* buccal ganglion. *l.n.* lateral nerve-cords. *a'.n.* œsophageal nerve. *p.c.* anterior pedal commissure. *p.c'.* roots of one of the succeeding pedal commissures. *p.n.* pedal nerve-cord.

commissure, though with greater difficulty, in *Cryptoplax striatus*. In a point of this kind it is not at all necessary that one or other of

[1] E. Brandt, "Ueber das Nervensystem von *Chiton fascicularis*": Bull. Acad. St. Petersb., xiii, 1869.

[2] H. v. Jhering, "Beiträge zur Kenntnis des Nervensystems der Amphineuren," etc.: Morph. Jahrb., iii, 1877, p. 157.

[3] Haller, "Der Chitonen der Adria." Pt. 1: Arb. Inst. Wien, iv, 1882, p. 7.

[4] No. 1305 D, Physiological Series, Roy. Coll. Surg. Museum.

the conflicting statements must be wrong; the probable explanation being that we have here one of those details in which different species vary from one another.

(*b*) *The pedal commissures.*—Here again, as regards the anterior pedal commissure, my observations uphold Von Jhering to the disadvantage of Haller: for the latter,[1] in contradiction to Von Jhering's[2] assertion that the anterior commissure considerably exceeds its successors in size, denies that it can be distinguished from the rest in any way. In *Hanleya abyssorum* the anterior pedal commissure is a simple unbranched strand passing directly from one pedal cord to the other (Fig. II, *p.c.*). In size it is about equal to the subœsophageal commissure, and is strikingly larger than its companions, for whereas they could only with difficulty be seen at their origin from the pedal nerves, the anterior commissure could be easily traced and removed.[3] The comparative difference in size between the anterior pedal commissure and the roots of its successors can be seen in Fig. II, *p.c.*, *p.c'*.

As we follow the pedal cords to their posterior extremity, we find that they gradually approach each other, till at the extreme end of the foot they appear to become continuous, forming a loop comparable to that made by the lateral cords above the rectum. In reality, however, this is not exactly the case, for the examination of a series of sections through this region makes it evident that a short tract uniting the two cords is devoid of ganglion cells, so that they must be said to be united by a short, stout, fibrous commissure (Fig. III, *c.*).

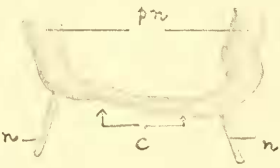

Fig. III.—Posterior extremity of the pedal nerve-cords of *Hanleya abyssorum*. × 30 (reconstructed from sections). *c.* fibrous commissure. *n.* nerves dipping into muscles of the foot (these nerves are about equal in size to the preceding pedal commissures). *p.n.* pedal nerve-cords.

(*c*) *The heart.*—The heart, in certain parts of its structure, seems to be a most interestingly variable organ in the different species of Chiton. From a paper published last year by Haller,[4] one can recognize no less than four different types dependent on the number and position of the auriculo-ventricular openings. At the bottom of the scale he describes four pairs of such openings in *Chiton magnificus*; then comes the condition found in most Chitons, two pairs; after that, one pair with

[1] *Loc. cit.* pt. 1, p. 12.

[2] Von Jhering, "Vergleichende Anatomie des Nervensystems und Phylogenie der Mollusken," p. 45.

[3] No. 1305C, Physiological Series, Roy. Coll. Surg. Museum.

[4] Haller, Morph. Jahrb., xxi, 1894, p. 29.